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Stress and recovery of hill pastures in the North Island of New Zealand

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Abstract

Moisture and treading treatments were imposed on intact turves that were relocated to a glasshouse after being removed from three hill pastures of different soil fertility in the North Island of New Zealand. The experiment consisted of a 2-month stress phase, where the treatments were wetting (W), wetting and treading (WT), drying (D) and control (C). In this phase, herbage accumulation rate, tiller density and leaf extension rate were lower on the D turves, and herbage accumulation rate and tiller density were lower on the WT turves than for the C turves. Herbage accumulation rate was higher on the W treatment than on the C treatment.

In the 2-month recovery phase, herbage accumulation rate and leaf extension rate on the D turves were higher than those of the C treatment. Herbage accumulation rate and tiller density took longer to recover on the WT turves but by the end of the recovery period tiller density on these turves exceeded that of the C turves and the original tiller densities on the WT turves. Changes (increase or decrease) in leaf extension rate were associated with the W treatment and tiller density with the WT treatment. Moisture was limiting on the D and C turves, but on the W and WT turves, where moisture was adequate for plant growth, nutrients were limiting, notably phosphorus on the W and WT turves and sulphur on the W turves.

The D treatment turves recovered very quickly once the stress was removed but the WT turves were slower to recover. Under the experimental conditions applied, the hill pasture turves were more resilient to the drying treatment than the wetting and treading treatment.

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Introduction

Both soil moisture content (Norris, 1982) and treading by livestock (Pande *et al.*, 2000) can influence herbage production. Soil moisture content and the extent of treading damage by livestock are also both affected by the slope and variability in aspect of hill country in New Zealand; soil moisture directly and treading through the effects of topography on sheep behaviour. These two stresses can act individually or interact to decrease aspects of plant growth such as leaf extension and tillering.

The supply of moisture to plants has been reported as the primary factor limiting the attainment of production potential in New Zealand pastures (Lancashire, 1984). Hsiao and Acevedo (1974) stated that, if a period of soil water deficit was long and intense enough, then almost any plant process could be affected. Various plant processes do, however, have different sensitivities to water stress and can, therefore, be indicators of the severity of the stress. The physiological process most sensitive to water stress is cell growth (Hsiao and Acevedo, 1974; Barker *et al.*, 1989). This is useful from an experimental point of view in that leaf elongation (a measure of cell expansion) can be measured easily, whereas some of the other processes influenced by moisture stress (e.g. protein synthesis) are technically more difficult to measure. Tiller number can also be used as an indicator of moisture stress (Norris, 1982; Barker *et al.*, 1989; Van Loo, 1992). Van Loo (1992) found tiller numbers to be on average proportionately 0·20 lower when grown at a water potential of −1·3 MPa compared with those grown at 0 MPa. Tiller density may be reduced through increased tiller death at low soil moisture contents (Sheehy *et al.*, 1975) and or through the reduction of new tiller growth (Perry and Larson, 1974).

Treading can influence plant growth both directly by damage to plants from animals' hooves and indirectly through damage to the soil. Edmond (1962) observed that treading of pasture can result in crushed and bruised leaves (particularly on dry soil) and on wet soils can lead to direct root damage, plant displacement, plant burial and mud on leaves. Poaching damage to soil can result in crust formation on the soil surface, loss of soil structure, lack of earthworms and anaerobic soil conditions (Edmond, 1962), all of which can contribute to decreased plant growth. Tillering of plants was identified as being negatively affected by sheep treading in the experiments carried out by Edmond (1958; 1962; 1964; 1974) and also recently in a cattle treading experiment by Pande *et al.* (2000). Tiller density, therefore, may be a useful indicator of the degree of treading damage that has occurred in a sward.

The ability of an ecosystem to show resilience after disturbance is critical to the survival of that ecosystem. Resilience is the term applied to natural ecosystems that have the ability to restore their structure following acute or chronic disturbance (natural or human-induced) (Westman, 1978). A resilient pasture is particularly important in New Zealand agricultural systems because of the dependence on a year-round supply of feed from these pastures. The ability of pastures to regain original production levels following a drought or a severe treading event in winter is essential. This paper aims to quantify both the production impediments that occur when a hill pasture is placed under moisture and treading stress and how these pastures recover when that stress is removed. The paper also aims to identify how the growth of hill pastures is affected when impacted by moisture or treading stress. The experimental approach was to use turves from pastures from farm systems with different management histories. Since environmental conditions are difficult to control or manipulate in the field (e.g. rainfall), turves were removed from the pastures to a controlled environment.

Materials and methods

Turf removal

A total of thirty-six blocks of intact turf and soil were lifted from existing pasture at Ballantrae Hill Research Station, a naturally low fertility, North Island, hill-country farm situated near Woodville, New Zealand (latitude 175°50′E, longitude 40°18′S), in early November 1996. The turves were 1 m long, 0·5 m wide and 0·4 m deep. Twelve turves were removed from each of three sites, which had a varied management history (Lambert *et al.*, 1996). The high fertility (HH) site had 37·5 kg P ha^{-1} year^{-1} applied as superphosphate since 1973, the second (HN) site had the same level of fertilizer applied until 1980, when fertilizer application ceased, and the third site (LN) had a low rate of fertilizer (12 kg P ha^{-1} year^{-1}) applied from 1973 until fertilizer application ceased in 1980. The stocking rates on the farmlets were adjusted to match pasture production.

The turves were removed from the sites using cutting apparatus mounted on a tractor (Newton *et al.*, 1994). The apparatus consisted of a cutting tool and a turf bin. A hole was initially dug in the soil deep enough to fit the cutting tool and a bin flush with the soil surface. Water was pumped from the cutting apparatus on to the sides of the bin to aid its movement through the soil. Guide wheels on the cutting apparatus controlled the depth of the turf. Once the turf bin was full, the turf was cut off using a sharpened spade, then lifted out of the channel using a second tractor. A new bin was then attached to the cutting apparatus. This procedure was repeated until twelve turves were obtained. Because of physical constraints, the turves were removed from relatively flat areas rather than steep slopes. Stock camps and tracks were avoided in the collection of turves.

The turves were lifted over a period of *c.* 2 weeks and were transported to the Plant Growth Unit at Massey University, Palmerston North, New Zealand (latitude 175°37′E, longitude 40°23′S). The turves remained outside for *c.* 1 week during which time sheet metal ends were attached to the bins, so that no bare soil was exposed. They were also hand-watered during this time. The turves were then randomly allocated to positions within a 25 × 12·5 m glasshouse, with three rows of twelve turves.

The turves were used in a prior experiment involving defoliation height and treading treatments (Nicholas, 1999). This experiment was carried out in the same glasshouse and the turves were rested for 3 months between experiments, during which time they were watered daily and trimmed weekly to a standard height of 50 mm. Fertilizer was applied at the beginning of the rest period to replace sulphur, phosphorus and nitrogen removed from the turves in herbage harvested. The total amount of herbage harvested during the prior experiment was calculated, the concentration of S, P and N in the removed herbage was estimated and superphosphate and urea applied to replace those nutrients removed.

The turves maintained their original differences in fertility developed at the sites at Ballantrae. There were twelve each of the high, medium and low fertility turves with Olsen P levels of 13·3, 8·2 and 6·3 respectively. Moisture and treading treatments were applied to these fertility treatments. The experiment comprised a treatment phase (2 months) and a recovery phase (2 months).

In phase 1, the treatment phase, three moisture and two treading treatments were applied between 11

September 1997 and 18 November 1997. The three moisture treatments were established on the turves using an automated watering system. Polythene shields were placed between adjacent turves to prevent water crossing between treatments. The heavy watering treatment involved maintaining the turves at a soil volumetric moisture content of *c.* 60 $cm^3\ cm^{-3}$ as determined by Time Domain Reflectometry (TDR) (Topp *et al.*, 1984). The control turves were maintained at a soil moisture content of *c.* 40 $cm^3\ cm^{-3}$ and the dry turves during this phase were unwatered, and dried from a soil moisture content of 60 $cm^3\ cm^{-3}$ to an average of *c.* 10 $cm^3\ cm^{-3}$.

The treading treatment (T) was heavy simulated sheep treading using a studded roller. This technique was developed by Awan (1995) and applied an average pressure of 1·28 mg m^{-3} to the soil surface with each pass. The turves received ten passes of the roller, applied after each cutting. This treatment was applied to half of the heavily watered turves.

In summary there were four treatments each applied to nine turves in phase 1: W, wet; WT, wet and treading; C, control; and D, dry.

In phase 2, the recovery phase (from 18 November 1997 to 31 January 1998), the wet treatment turves were allowed to dry until they reached the soil moisture content of the control treatment (volumetric soil moisture content of 40 $cm^3\ cm^{-3}$), and the dry treatment turves were wet through until they reached the soil moisture content of the control treatment. Both treatments took *c.* 10 d to reach the desired soil moisture contents. The treading treatment ceased on the WT treatment turves at the same time as the water treatment. This was to simulate the removal of animals from a waterlogged and poached pasture to aid its recovery. During both phases, the sward was maintained by weekly cutting to a height of 50 mm.

Measurements

Botanical measurements

The contribution of individual species to herbage mass (kg DM ha^{-1}) was determined for a 0·01 m^2 area (cut to ground level) at the centre of each turf. Two dissections that separated all species present were carried out. The first was taken at the start of phase 1 on 11 September 1997. The same technique was used at the end of phase 2 in February 1998, but a 0·11 m^2 area was used as the turves were not required for further experimentation.

Once a week the turves were trimmed with electric shears to a height of 50 mm to simulate defoliation by grazing animals. Cut herbage was collected, dried and weighed to determine herbage accumulation rate (kg DM $ha^{-1}\ d^{-1}$) above 50 mm over that period.

Leaf extension rate (mm d^{-1}) was measured on the most common and agronomically important species present. These species were: *Lolium perenne*, *Agrostis capillaris*, *Holcus lanatus*, *Anthoxanthum odoratum* and *Trifolium repens*. Leaf extension rate was measured over a period of 5 d every 4 weeks. On each turf, one tiller of each species was tagged with an identifying coloured tag. The length of the youngest leaf was measured from the collar of the most recently fully expanded leaf to the tip, and then over the subsequent days was re-measured. If the leaf died or ceased growing over the 5-d period, the new leaf that emerged was measured.

On each turf, the tillers or growing points were counted monthly in three 0·025 m^2 quadrats and then averaged (tillers m^{-2}).

Two root samples were taken, one in each phase. In early September 1997, two 30 cm deep soil cores (332 cm^3) were removed from each turf, discarded, and the holes backfilled with clean dry sand. At the end of phase 1 (17 November 1997), the sand-filled cores were removed, the roots collected by hand and washed. Root length and root weight of the roots grown in phase 1 were then determined.

Two more cores were taken at the end of the second phase (4 February 1998) and the same method used to determine the length and weight of roots grown in phase 2.

Soil measurements

In late November 1997, early in the recovery phase, soil samples were removed from each turf and a 2 M KCl-extractable nitrate procedure (Blakemore *et al.*, 1987) used to determine the concentration of NH_4^+ and NO_3^- (ppm). Soil cores were taken to a depth of 75 mm and the core diameter was 25 mm.

Soil samples were taken from the turves at the beginning of the experiment to identify if any changes had occurred in fertility between the first and second turves experiments. P, S and pH were measured for all thirty-six turves. Soil temperature measurements were made weekly on each turf using a 0·1 m soil temperature probe in five fixed positions. The five measurements were then averaged for the turf. Soil moisture was measured using TDR (Topp *et al.*, 1984). Two 0·2 m probes were permanently placed in the centre of each turf and monitored twice weekly.

Statistical analysis

The experiment was a 3 × 4 factorial with three blocks. The design was blocked as the glasshouse in which the turves were located had doors at either end, which may have impacted on ambient temperature and humidity across the turves. A basic ANOVA was carried out on all data using the PROC GLM command of the SAS programme (SAS, 1995). The model used for the ANOVA was:

$$Y_{ijk} = \mu + b_k + f_i + s_j + (fs)_{ij} + \varepsilon_{ijk},$$

where μ is the overall mean, b_k is the block effect, f is the farmlet effect, s is the applied stress affect, fs is the interaction and ε is the unknown error.

Duncan's multiple range test and Tukey's studentized range (HSD) test (SAS, 1995) were used to compare differences between treatments.

Results

Environmental changes in response to moisture stress treatments

From 11 September 1997 to 17 November 1997 (the stress phase) the stress treatments resulted in different soil moisture contents ($P < 0{\cdot}001$ for all months) (Figure 1). The D turves consistently had the lowest soil moisture content in this phase. From 18 November 1997 to January 1998 (the recovery phase) none of the turves had significantly different soil moisture contents. Site had a significant ($P < 0{\cdot}05$) effect on soil moisture content in the first half of November at peak stress (Table 1). The sites were ranked LN, HN and HH from highest soil moisture content to lowest. There were no significant interactions between stress treatment and site.

In all months except January, soil temperatures were significantly ($P < 0{\cdot}05$) different in the stress treatments (Table 2). In the stress phase, the W and WT treatment turves had lower soil temperatures than the C or D treatment turves. Initially in the recovery phase, the W turves had a higher soil temperature and the D turves a lower soil temperature than the WT and C turves, which did not differ. As the recovery phase progressed, the D turves increased in soil temperature, reaching the same temperature as the C, W and WT turves in January. There were no significant interactions of site or stress treatment on soil temperature.

Soil pH and Olsen P values and NO_3^- contents were not different between moisture stress treatments (Table 3). Differences between these treatments occurred for soil sulphur and NH_4^+ contents ($P = 0{\cdot}06$) (Table 3). Soil pH differed among sites ($P < 0{\cdot}05$) with the LN site having the highest and the HH site the lowest. Soil S content was different between sites ($P < 0{\cdot}001$) with the HH site having the highest soil sulphur content and the HN site the lowest. Olsen P values were different between sites ($P < 0{\cdot}001$) with the HH site having the highest Olsen P and the LN site the lowest (Table 3). Soil NO_3^- and NH_4^+ contents did not differ between sites. There were no interactions between treatments and sites for soil nutrient variables.

Herbage accumulation

Moisture stress treatment effects on herbage accumulation did not become significant until October 1997 but they remained significant for the rest of the experimental period (Table 4a). In the stress phase and early recovery phase, the W treatment turves accumulated

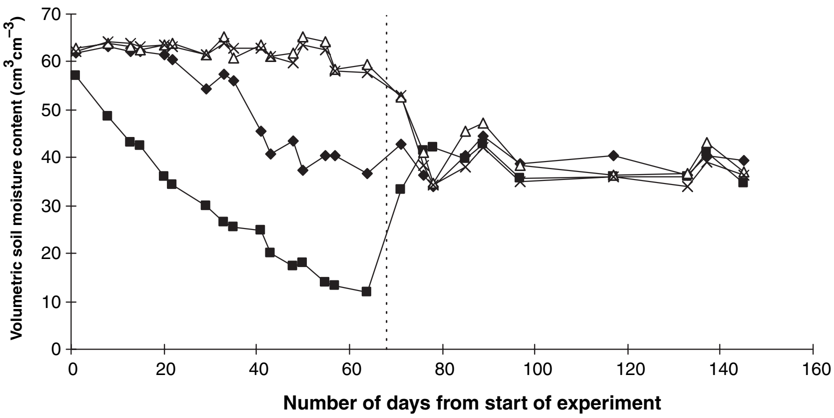

Figure 1 Volumetric soil moisture content (cm^3 cm^{-3}) of the stress treatment turves [◆, C = control, maintained at a volumetric soil moisture content (VMSC) of 40 cm^3 cm^{-3} from 11 September 1997 to 31 January 1998; ■, D = dry, maintained at VSMC of 10 cm^3 cm^{-3} from 11 September 1997 to 17 November 1997 and then the same as C until 31 January 1998; △, W = wet, maintained at VSMC of 60 cm^3 cm^{-3} from 11 September 1997 to 17 November 1997 and then the same as C until 31 January 1998 and ×, WT = wet and treading, maintained at VSMC of 60 cm^3 cm^{-3} with simulated livestock treading applied from 11 September 1997 to 17 November 1997 and then the same as C until 31 January 1998] over the experimental period (days 0–145). The dotted line indicates when the experiment changed from phase 1 (stress phase) to phase 2 (the recovery phase).

Table 1 Volumetric soil moisture content ($cm^3\ cm^{-3}$) for the three sites from 11 September 1997 to 31 January 1998.

Month	Sites LN	HN	HH	s.e. of mean	Level of significance
September 1997	57·6	52·9	56·2	1·46	NS†
October 1997	52·5	48·7	50·4	1·17	NS
November A 1997‡	45·4	42·7	41·3	0·94	*
November B 1997‡	43·1	38·8	39·1	1·38	NS
December 1997	42·7	39·2	40·0	1·92	NS
January 1998	38·2	36·1	38·9	1·66	NS

*$P < 0·05$.

†NS, not significant.

‡A is the stress phase (first half of November) and B is the recovery phase (second half of November).

LN, 12 kg P ha^{-1} $year^{-1}$ applied as superphosphate from 1973 until 1980; HN, 37·5 kg P ha^{-1} $year^{-1}$ applied as superphosphate from 1973 until 1980; HH, 37·5 kg P ha^{-1} - $year^{-1}$ applied as superphosphate continuously since 1973.

Table 2 Soil temperature (°C) for the four stress treatments from 11 September 1997 to 31 January 1998.

Month	Stress treatments C	D	W	WT	s.e. of mean	Level of significance
September 1997	14·3	14·6	14·3	14·0	0·10	**†
October 1997	16·6	16·6	16·0	15·8	0·11	***
November A 1997‡	16·6	17·0	16·1	16·0	0·07	***
November B 1997‡	19·0	17·4	19·4	19·1	0·09	***
December 1997	19·3	19·5	19·8	19·3	0·18	*
January 1998	20·9	20·9	21·1	20·9	0·07	NS

*$P < 0·05$; **$P < 0·01$; ***$P < 0·001$.

†NS, not significant.

‡A is the stress phase (first half of November) and B is the recovery phase (second half of November).

C, control, maintained at a volumetric soil moisture content (VMSC) of 40 $cm^3\ cm^{-3}$ from 11 September 1997 to 31 January 1998; D, dry, maintained at VSMC of 10 $cm^3\ cm^{-3}$ from 11 September 1997 to 17 November 1997 and then the same as C until 31 January 1998; W, wet, maintained at VSMC of 60 $cm^3\ cm^{-3}$ from 11 September 1997 to 17 November 1997 and then the same as C until 31 January 1998; WT, wet and treading, maintained at VSMC of 60 $cm^3\ cm^{-3}$ with simulated livestock treading applied from 11 September 1997 to 17 November 1997 and then the same as C until 31 January 1998.

significantly ($P < 0·05$) more herbage above 50 mm than the other treatments and the D treatment turves significantly ($P < 0·05$) less than the other treatments. Late in the recovery phase, the D treatment turves had significantly ($P < 0·05$) higher herbage accumulation rates above the 50 mm cutting height than the other treatments and the WT turves had a significantly ($P < 0·05$) lower herbage accumulation rate than the other treatments (Figure 2).

In all months, except November, the site from which the turf was removed had a significant influence on herbage accumulation above the cutting height of 50 mm (Table 4b). From August to October, the HH turves had significantly ($P < 0·01$) higher herbage accumulation rates than the other treatments and the LN turves had significantly ($P < 0·01$) lower herbage accumulation rates than the other treatments. In January, the HH turves accumulated significantly ($P < 0·05$) more herbage mass than the other treatments and the HN turves significantly ($P < 0·05$) less than the other treatments.

Interactions between site and stress treatment were only significant ($P < 0·05$) at the peak of the stress period (first half of November). Herbage accumulation

Table 3 Values of pH and soil nutrient measurements (ppm) taken in August 1997 in relation to (a) stress treatments and (b) sites.

	(a) Stress treatments					
Month	C	D	W	WT	s.e. of mean	Level of significance
pH	5·60	5·64	5·69	5·57	0·036	NS†
Sulphur content	19·8	14·9	13·4	18·9	1·92	NS
Olsen P content	9·4	9·3	8·4	9·7	1·07	NS
NO_3^- content	0·50	0·44	0·46	0·46	0·046	NS
NH_4^+ content	1·74	1·36	1·82	1·60	0·132	NS

	(b) Sites				
Month	LN	HN	HH	s.e. of mean	Level of significance
pH	5·68	5·62	5·57	0·047	*
Sulphur content	13·5	10·3	26·5	1·66	**
Olsen P content	6·3	8·2	13·3	0·93	**
NO_3^- content	0·43	0·45	0·51	0·053	NS
NH_4^+ content	1·63	1·52	1·74	0·114	NS

*$P < 0·05$; **$P < 0·001$.

†NS, not significant.

C, control, maintained at a volumetric soil moisture content (VMSC) of 40 $cm^3\ cm^{-3}$ from 11 September 1997 to 31 January 1998; D, dry, maintained at VSMC of 10 $cm^3\ cm^{-3}$ from 11 September 1997 to 17 November 1997 and then the same as C until 31 January 1998; W, wet, maintained at VSMC of 60 $cm^3\ cm^{-3}$ from 11 September 1997 to 17 November 1997 and then the same as C until 31 January 1998; WT, wet and treading, maintained at VSMC of 60 $cm^3\ cm^{-3}$ with simulated livestock treading applied from 11 September 1997 to 17 November 1997 and then the same as C until 31 January 1998.

LN, 12 kg P $ha^{-1}\ year^{-1}$ applied as superphosphate from 1973 until 1980; HN, 37·5 kg P $ha^{-1}\ year^{-1}$ applied as superphosphate from 1973 until 1980; HH, 37·5 kg P $ha^{-1}\ year^{-1}$ applied as superphosphate continuously since 1973.

rate above 50 mm on the W treatment with the LN turves (9·9 kg DM $ha^{-1}\ d^{-1}$) was *c.* 0·50 that on the W treatment with the HN turves (15·4 kg DM $ha^{-1}\ d^{-1}$) and W treatment with the HH turves (17·4 kg DM $ha^{-1}\ d^{-1}$).

Herbage accumulation rate above 50 mm was greater in the recovery phase than the stress phase (Figure 2) and the rate of herbage accumulation in the recovery phase differed between treatments. From Figure 2 it can be seen that the recovery phase can be divided into two stages, days 3–24 and days 24–65.

An ANOVA was carried out for days 3, 24 and 65 to determine if herbage accumulation rates were different between the stress treatments (Table 5a). At day 3 in the recovery phase the D treatment turves had a significantly ($P < 0·05$) lower herbage accumulation rate than the other treatments but, by day 65, the D turves had a significantly ($P < 0·05$) higher herbage accumulation rate above 50 mm than the other treatments.

Another analysis was performed to determine if the change in herbage accumulation rate between days 3 and 24, 24 and 65, and 3 and 65 differed between stress treatments (Table 5b). For the D treatment turves, the change in herbage accumulation rate between days 3 and 24 was greater ($P < 0·001$) than for any other treatment. Between days 24 and 65 the change in herbage accumulation was similar for all treatments, with the exception of the control, which had significantly ($P < 0·05$) greater increases in herbage accumulation rate than the other treatments. Over the whole recovery phase (days 3–65), the D turves exhibited the largest change in herbage accumulation rate and the WT turves the smallest (Table 5b).

Physiological changes in response to moisture stress treatments

In the stress phase, root length was significantly ($P < 0·05$) higher in the W treatment turves (95 560 m m^{-3}) than the other treatments and significantly ($P < 0·05$) lower on the D treatment turves (51 110 m m^{-3}) than on the other treatments.

In the recovery phase, the stress treatments had a significant effect on root weight with the C treatment turves having a significantly ($P < 0·05$) greater root weight than the D treatment turves (152 and 64 g m^{-3} respectively). Neither the W nor WT treatment turves (125 and 117 g m^{-3} respectively) significantly differed from the C or D treatment turves. Both site ($P < 0·05$) and stress treatments ($P < 0·05$) had a significant effect on root length. The sites were ranked LN

Table 4 Herbage dry matter accumulated above the cutting height of 50 mm (kg ha^{-1} d^{-1}) for (a) stress treatments and (b) sites.

	(a) Stress treatments					
Month	**C**	**D**	**W**	**WT**	**s.e. of mean**	**Level of significance**
August 1997	11·6	11·0	10·9	10·2	1·14	NS†
September 1997	12·0	13·2	13·6	13·1	0·84	NS
October 1997	11·5	7·4	13·2	8·8	0·79	***
November A 1997‡	6·7	3·4	14·3	6·7	0·75	***
November B 1997‡	5·5	3·0	12·2	7·1	1·16	***
December 1997	16·2	33·3	28·3	14·8	1·87	***
January 1997	24·8	32·6	31·6	20·4	2·36	**

	(b) Sites				
Month	**LN**	**HN**	**HH**	**s.e. of mean**	**Level of significance**
August 1997	8·8	10·3	13·7	0·99	**
September 1997	10·6	11·8	16·5	0·73	***
October 1997	8·6	9·6	12·4	0·69	**
November A 1997	7·0	7·9	8·4	0·65	NS
November B 1997	6·1	6·8	7·9	1·00	NS
December 1997	24·9	20·1	24·5	1·62	NS
January 1997	27·3	23·3	31·4	2·04	*

*$P < 0·05$; **$P < 0·01$; ***$P < 0·001$.

†NS, not significant.

‡A is the stress phase (first half of November) and B is the recovery phase (second half of November).

C, control, maintained at a volumetric soil moisture content (VMSC) of 40 cm^3 cm^{-3} from 11 September 1997 to 31 January 1998; D, dry, maintained at VSMC of 10 cm^3 cm^{-3} from 11 September 1997 to 17 November 1997 and then the same as C until 31 January 1998; W, wet, maintained at VSMC of 60 cm^3 cm^{-3} from 11 September 1997 to 17 November 1997 and then the same as C until 31 January 1998; WT, wet and treading, maintained at VSMC of 60 cm^3 cm^{-3} with simulated livestock treading applied from 11 September 1997 to 17 November 1997 and then the same as C until 31 January 1998.

LN, 12 kg P ha^{-1} $year^{-1}$ applied as superphosphate from 1973 until 1980; HN, 37·5 kg P ha^{-1} $year^{-1}$ applied as superphosphate from 1973 until 1980; HH, 37·5 kg P ha^{-1} $year^{-1}$ applied as superphosphate continuously since 1973.

(58 750 m m^{-3}) ≥ HH (53 167 m m^{-3}) > HN (28 333 m m^{-3}) for their effect on root length. The stress treatments were ranked C (59 353 m m^{-3}) ≥ WT (49 556 m m^{-3}) ≥ W (49 333 m m^{-3}) > D (28 778 m m^{-3}) for their influence on root length.

In October and November 1997, the stress treatments had a significant ($P < 0·05$) effect on tiller density with both the WT and D treatments having lower tiller densities than the C and W treatments (Table 6a). Site influenced tiller density in all months (Table 6b). HH turves produced significantly ($P < 0·05$) more tillers than either the HN or LN turves, which did not differ. There were no interactions between site and stress treatment for tiller density.

Stress treatments significantly ($P < 0·05$) affected leaf extension rate from October to the end of the experiment in October 1997. Leaf extension rate was significantly ($P = 0·001$) higher on the W treatment turves than the D and C treatments, but not the WT treatment. Leaf extension rate was significantly ($P < 0·001$) lower on the D treatment turves than on the other treatments (Table 7a). Throughout the recovery phase, the D treatment turves had a significantly ($P < 0·05$) higher leaf extension rate than the other treatments (Table 7a).

Site effects did not begin to have a significant effect on leaf extension rate until November 1997, but they then remained significant through December and January ($P < 0·01$ and $P < 0·05$ respectively). The HH turves consistently had a higher rate of leaf extension than the LN turves although they were not significantly higher than HN turves in any month (Table 7b).

Factors influencing herbage accumulation rate for each of the treatments in the late stress period

For each treatment, a range of factors, including volumetric soil moisture content, soil temperature, soil

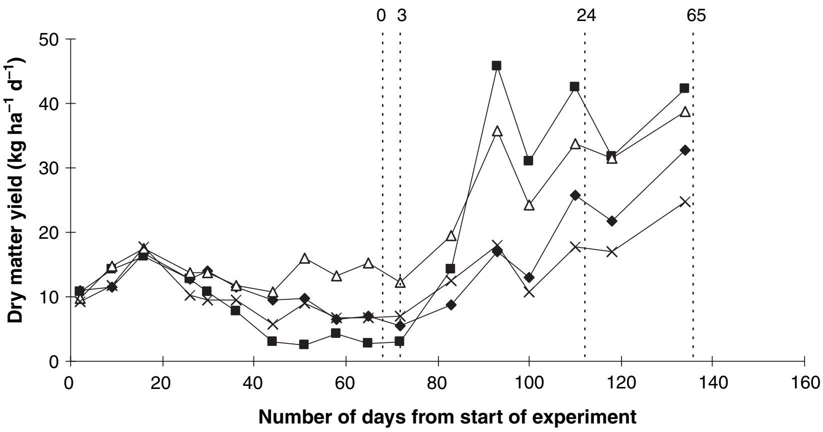

Figure 2 Dry-matter (DM) yield (kg ha^{-1} d^{-1}) from the stress treatment turves [♦, C = control, maintained at a volumetric soil moisture content (VMSC) of 40 cm^3 cm^{-3} from 11 September 1997 to 31 January 1998; ■, D = dry, maintained at VSMC of 10 cm^3 cm^{-3} from 11 September 1997 to 17 November 1997 and then the same as C until 31 January 1998; △, W = wet, maintained at VSMC of 60 cm^3 cm^{-3} from 11 September 1997 to 17 November 1997 and then the same as C until 31 January 1998 and ×, WT = wet and treading, maintained at VSMC of 60 cm^3 cm^{-3} with simulated livestock treading applied from 11 September 1997 to 17 November 1997 and then the same as C until 31 January 1998] over the experimental period. The area of the graph between the dotted lines labelled '0' and '65' represents the days of the recovery phase.

Table 5 (a) Rates of herbage accumulation (kg DM ha^{-1} d^{-1}) under each stress treatment during different stages of the recovery phase and (b) differences in the rates of herbage accumulation (kg DM ha^{-1} d^{-1}) at key stages during the recovery phase.

	Stress treatments				s.e. of difference	Level of significance
	C	D	W	WT		
(a) Days after start of recovery period						
3	5·5	2·9	12·2	7·1	1·58	***†
24	17·1	45·7	35·7	18·0	4·15	***
65	32·6	42·2	38·7	24·7	4·96	**
(b) Sections of recovery period (days)						
3–24	11·6	42·7	23·6	10·9	4·10	***
24–65	15·5	-3·4	2·9	6·7	5·38	*
3–65+	27·1	39·2	26·5	17·6	4·94	**

*$P < 0·05$; **$P < 0·01$; ***$P < 0·001$.

†NS, not significant.

Olsen P and soil S content, were regressed against herbage accumulation rate to identify which factors had the greatest influence on herbage accumulation rate in the late stages of the stress phase (October and early November 1997).

Volumetric soil moisture content exhibited a significantly ($P < 0·001$) positive correlation with herbage accumulation rate on the C and D turves (Table 8), soil temperature exhibited a significantly ($P < 0·01$) negative correlation with herbage accumulation rate on the D and WT turves, soil Olsen P exhibited a significantly ($P < 0·01$) positive correlation with herbage accumulation rate on the W and WT turves and soil S content exhibited a significantly ($P < 0·01$) positive correlation with herbage accumulation on the W turves.

Discussion

Stress phase

For approximately the first 20 d of the stress phase, the treatments had similar herbage accumulation rates. From day 20 until the end of the stress phase the treatments differentiated and, for the majority of the phase, the D turves had the lowest herbage accumulation rate and the W turves the highest. This reduction in herbage accumulation rate on the D turves was most likely because of the decrease in leaf extension rates and tiller density. On the W treatment turves (volumetric soil moisture content of 60 cm^3 cm^{-3}) the extra water available (above the 40 cm^3 cm^{-3} volumetric soil moisture content on the control turves) may have been

Table 6 Tiller density (tiller number m^{-2}) for (a) stress treatments and (b) sites.

	(a) Stress treatments					
Month	**C**	**D**	**W**	**WT**	**s.e. of mean**	**Level of significance**
September 1997	12 548	12 874	14 859	12 548	929	NS†
October 1997	14 444	11 333	16 059	10 696	941	*
November 1997	13 956	9274	15 807	11 807	765	**
December 1997	12 711	14 089	15 096	14 385	1053	NS
January 1998	14 385	15 274	13 689	19 067	1698	NS

	(b) Sites				
Month	**LN**	**HN**	**HH**	**s.e. of mean**	**Level of significance**
September 1997	12 378	11 511	15 733	805	*
October 1997	11 967	11 244	16 189	815	**
November 1997	11 433	11 500	15 200	662	**
December 1997	11 478	12 033	18 700	911	**
January 1997	13 111	13 167	20 533	1470	*

*$P < 0{\cdot}01$; **$P < 0{\cdot}001$.

†NS, not significant.

C, control, maintained at a volumetric soil moisture content (VMSC) of 40 cm^3 cm^{-3} from 11 September 1997 to 31 January 1998; D, dry, maintained at VSMC of 10 cm^3 cm^{-3} from 11 September 1997 to 17 November 1997 and then the same as C until 31 January 1998; W, wet, maintained at VSMC of 60 cm^3 cm^{-3} from 11 September 1997 to 17 November 1997 and then the same as C until 31 January 1998; WT, wet and treading, maintained at VSMC of 60 cm^3 cm^{-3} with simulated livestock treading applied from 11 September 1997 to 17 November 1997 and then the same as C until 31 January 1998.

LN, 12 kg ha^{-1} $year^{-1}$ applied as superphosphate from 1973 until 1980; HN, 37·5 kg P ha^{-1} $year^{-1}$ applied as superphosphate from 1973 until 1980; HH, 37·5 kg P ha^{-1} $year^{-1}$ applied as superphosphate continuously since 1973.

utilized by the plants for increased rates of leaf extension, which is directly affected by soil moisture content (Hsiao and Acevedo, 1974; Norris, 1982; Barker *et al.*, 1985). This effect may have been accentuated in the glasshouse as the experiment proceeded as temperatures both outside and inside the glasshouse increased with the approach of summer. Having a volumetric soil moisture content of 60 cm^3 cm^{-3} may have alleviated heat stress that could have occurred on the turves with the lower volumetric soil moisture content of 40 cm^3 cm^{-3} (control turves). In the late stress phase (October/November) soil temperatures on the W and WT treatment turves did not differ but they were significantly lower than soil temperatures on the C and D treatment turves (Table 2). Davies and Thomas (1983) found that supra-optimal temperatures, as well as a low water potential, played a role in reducing leaf appearance rate.

The WT turves had lower herbage accumulation rates than the W and C turves. Similar effects of treading have been observed by Edmond (1958; 1962; 1964; 1974), Carter and Sivalingam (1977), Witschi and Michalk (1979), Sheath and Carlson (1998), Betteridge *et al.* (1999) and Pande *et al.* (2000). The mechanisms for this reduction in herbage accumulation rate with treading could include reduction in tiller number and vigour, physical damage to plants causing a decrease in photosynthetic area and efficiency, and reduced transpiration and gaseous diffusion rates. In this experiment, tiller density on the WT turves was significantly lower than on the W turves (Table 6) and this may be one factor contributing to lower herbage accumulation on the WT turves. In field experiments on treading, Pande *et al.* (2000) found that other factors (in addition to reduced tiller number) that may reduce herbage accumulation are a decrease in leaf area index and reduced canopy cover. Data to support these findings were not collected in this experiment. The reduction in herbage accumulation rates with treading is significant as ultimately it means there is less feed available for livestock.

Tiller density was lower on the D turves compared with the control turves during the stress phase, and a regression between volumetric soil moisture content and tiller number was significant and positive. This finding is supported by Barker *et al.* (1985), who found that the tiller density of perennial ryegrass was reduced under moisture stress. Norris (1982) found a varying extent of tiller reduction under moisture stress, with varieties of hybrid ryegrass and tall fescue exhibiting a

Table 7 Leaf extension data (mm d^{-1}) for (a) stress treatments and (b) sites.

	(a) Stress treatments					
Month	**C**	**D**	**W**	**WT**	**s.e. of mean**	**Level of significance**
September 1997	3·7	3·1	3·2	3·2	0·3	NS†
October 1997	3·1	0·4	4·7	4·0	0·4	***
November 1997	2·7	7·7	4·7	3·9	0·5	***
December 1997	3·1	5·8	4·2	3·0	0·4	***
January 1998	5·4	7·9	5·2	6·4	0·6	*

	(b) Sites				
Month	**LN**	**HN**	**HH**	**s.e. of mean**	**Level of significance**
September 1997	3·1	3·1	3·6	0·3	NS
October 1997	3·0	2·8	3·3	0·3	NS
November 1997	3·7	4·7	5·8	0·5	NS
December 1997	3·1	4·2	4·8	0·4	**
January 1997	5·3	6·0	7·4	0·5	*

*$P < 0·05$; **$P < 0·01$; ***$P < 0·001$.

†NS, not significant.

C, control, maintained at a volumetric soil moisture content (VMSC) of 40 cm^3 cm^{-3} from 11 September 1997 to 31 January 1998; D, dry, maintained at VSMC of 10 cm^3 cm^{-3} from 11 September 1997 to 17 November 1997 and then the same as C until 31 January 1998; W, wet, maintained at VSMC of 60 cm^3 cm^{-3} from 11 September 1997 to 17 November 1997 and then the same as C until 31 January 1998; WT, wet and treading, maintained at VSMC of 60 cm^3 cm^{-3} with simulated livestock treading applied from 11 September 1997 to 17 November 1997 and then the same as C until 31 January 1998.

LN, 12 kg P ha^{-1} $year^{-1}$ applied as superphosphate from 1973 until 1980; HN, 37·5 kg P ha^{-1} $year^{-1}$ applied as superphosphate from 1973 until 1980; HH, 37·5 kg P ha^{-1} $year^{-1}$ applied as superphosphate continuously since 1973.

significant decrease in tiller number per plant but cocksfoot only showing a slight decrease. This reduction in tiller number with increasing moisture deficit may have been brought about by two mechanisms. The first is the increased rate of tiller death under drought conditions. Sheehy *et al.* (1975) found that, when the leaf water potential of *L. perenne* was allowed to fall to −1·5 MPa, the mass of dead tillers increased to 0·50 of total herbage mass of dry matter (DM). The other mechanism is through reduction in new tiller growth. Perry and Larson (1974) showed in *Medicago sativa* that the reduction of soil water to 0·50 of field capacity reduced both the number of primary shoots and the re-growth of shoots after defoliation. Van Loo (1992) found that a low water potential reduced tillering rates of perennial ryegrass considerably by temporarily reducing leaf appearance rate to about 0·85 of the control treatment. Leaf appearance rate is linked to tiller bud formation because, in the axil of each leaf, one tiller bud is formed. Both these mechanisms are designed to reduce total plant leaf area from which evapo-transpiration can occur, hence reducing water loss from the plant.

Leaf extension rate decreased significantly in the stress phase on the D treatment turves compared with the control turves. Cell growth or expansion is the most sensitive of the plant processes to water stress, because of its dependence on turgor pressure (Hsiao and Acevedo, 1974). High turgor pressure is required for cell expansion because the structural characteristics of the cell wall do not permit extension when turgor pressure falls below a threshold value. This threshold value varies between species but Turner and Begg (1978) suggested that leaf extension for most pasture species will be markedly decreased at a leaf water potential below 0·4 MPa. The range of turgor pressures allowing cell expansion can be narrow (Boyer, 1973) which makes leaf extension sensitive to moisture fluctuations. Most species, for example, will cease leaf elongation completely at leaf water potentials of −1 MPa (Turner and Begg, 1978). This range also varies for different species (Turner and Begg, 1978) and is one of the mechanisms species use to cope with water deficits. Van Loo (1992) found that at −1·3 MPa, the leaf extension rate of perennial ryegrass was 0·36 lower than at 0 MPa. The W and WT treatment turves probably did not have cell division and leaf extension limited by soil moisture hence their leaf extension rates in the stress phase were higher than those on the control and D treatment turves. From the results on the

Table 8 Correlation analyses of herbage accumulation rate and four environmental factors, for each stress treatment.

	Soil moisture vs. herbage accumulation rate		Soil temperature vs. herbage accumulation rate		Olsen P content vs. herbage accumulation rate		Soil sulphur content vs. herbage accumulation rate	
	Correlation coefficient	Level of significance	Correlation coefficient	Level of significance	Correlation coefficient	Level of significance	Correlation coefficient	Level of significance
C	0·55	***	−0·26	NS	0·1590	NS	0·0568	NS
D	0·51	***	−0·54	***	−0·0016	NS	0·1184	NS
W	0·09	NS	0·10	NS	0·6210	***	0·3514	**
WT	0·21	NS	−0·35	**	0·3857	**	0·0030	NS

$^{**}P < 0{\cdot}01$; $^{***}P < 0{\cdot}001$.

†NS, not significant.

C, control, maintained at a volumetric soil moisture content (VMSC) of 40 cm^3 cm^{-3} from 11 September 1997 to 31 January 1998; D, dry, maintained at VSMC of 10 cm^3 cm^{-3} from 11 September 1997 to 17 November 1997 and then the same as C until 31 January 1998; W, wet, maintained at VSMC of 60 cm^3 cm^{-3} from 11 September 1997 to 17 November 1997 and then the same as C until 31 January 1998; WT, wet and treading, maintained at VSMC of 60 cm^3 cm^{-3} with simulated livestock treading applied from 11 September 1997 to 17 November 1997 and then the same as C until 31 January 1998. Data from the late stress phase (1 November 1997–18 November 1997) were used for analyses.

leaf extension rate and tillering rate, it can be concluded that moisture had a greater influence on leaf extension rate and treading a greater effect on tillering rate.

Root length in the stress phase and root length and weight in the recovery phase, were lower for the D treatment turves than the other treatments indicating that the moisture deficit stress had a negative effect on root biology. The lower root weight and length suggested that either root death was increased or the growth of new roots was slowed by the moisture deficit or some other factor influenced by the moisture deficit. Gales (1979) suggested that in some circumstances the availability of phosphorus rather than the availability of water may influence the root:shoot ratio under drought conditions. The availability of phosphorus under the drought conditions imposed was not specifically tested in this experiment. The root length and weight were lower on the D treatment turves in the recovery phase than the other treatments, although the turves were fully watered, indicates that root growth takes time to recover from a period of drought. Long-term measurements would have indicated how long this suppression of root growth lasted. Vogt *et al.* (1993) suggested that fine roots may be useful indicators of stress. Fine roots are in direct contact with the soil and, hence, are the first point of contact for the plant with any soil-based environmental stresses (e.g. moisture or nutrient stress). They have also evolved to buffer or ameliorate environmental changes so that changes in the roots may not necessarily be seen in the aboveground part of the plant. Finally, because fine roots are an extremely dynamic part of the plant with varying rates of tissue turnover, they can respond rapidly to stress (Vogt *et al.*, 1993).

Recovery phase

In the recovery phase, the release of the D treatment turves from moisture stress resulted in increased rates of herbage accumulation. The recovery phase consisted of two distinct periods, the initial flush of growth that occurred immediately following the removal of the moisture stress (3–24 d) and the second period (24–65 d after treatment cessation) when all herbage accumulation rates of the treatments slowed and became similar. In addition to the removal of the moisture stress, NH_4^+ and NO_3^- can be released upon re-wetting of dry soil, which can also result in increased growth. Concentrations of these were measured in the soil *c.* 1 month after the change-over period and only a marginal difference in the concentration of NH_4^+ was observed between the treatments, and the D turves had the lowest concentration of NH_4^+. It is possible that the release of these nutrients had occurred and had been absorbed by the plants or soil organisms by the time the measurements were carried out. During recovery, the D treatment turves exhibited an increase in tiller number and tiller number was greater at the end of the recovery period than at the start of the experiment in September. Leaf extension rates on the D treatment turves also exhibited a compensatory effect by having higher than initial leaf extension rates and higher leaf extension rates than any of the other treatments. Such compensatory growth is proposed to come from rapid expansion of cells that continued to divide during a water deficit (Turner and Begg, 1978). These findings are similar to those of Barker *et al.* (1985) who found that yields from previously drought-stressed swards were greater, on removal of that drought stress, than previously irrigated swards. This compensatory growth was attributed to faster rates of tiller appearance, leaf appearance and leaf extension. The compensatory growth seen in this experiment and that of Barker *et al.* (1985) may also be dependent on higher concentrations of soluble sugars in the plant. Barlow *et al.* (1976), Horst and Nelson (1979) and Barker *et al.* (1985) found that compensatory growth on the removal of the moisture stress occurred in association with higher concentrations of soluble sugars, and these levels of soluble sugars may be required for compensatory growth to occur.

The release of the W treatment turves from excessive moisture stress also resulted in increased rates of herbage accumulation. An increase in soil temperature occurred on the W treatment turves in the recovery phase of the experiment (Table 2) and may have contributed to increased herbage accumulation rates. The drying out of the turves may have also resulted in increased oxygenation of the soil. Eccles *et al.* (1990) noted that water-logging caused decreased leaf extension rates and increased senescence rates in *Bromus willdenowii*, and Trought and Drew (1980) noted similar symptoms in water-logged wheat. Trought and Drew (1980) concluded that the reduction in leaf extension rate in waterlogged plants may be the result of a reduction in water uptake associated with low oxygen concentrations around the roots. This process is likely to be partially responsible for the increase in growth seen on the W treatment turves in the recovery phase with the removal of excess moisture.

Herbage accumulation on the WT turves was the lowest of any treatment in the recovery phase. This indicated that, even on cessation of the treading treatment, the treading effects suppressed herbage accumulation rate.

Limiting factors

The results presented in Table 8 suggest that water was limiting herbage accumulation rate in the C and D treatment turves, but not the W and WT treatment turves. However, nutrients were limiting herbage accumulation rate on the W and WT turves. Soil Olsen P and sulphur contents were positively associated with herbage accumulation rate on the W turves, but only Olsen P was positively associated with herbage accumulation rate on the WT turves. The S content was limiting on the W turves and not the WT turves may have been due to higher initial concentrations of S on the WT turves (Table 3), or a greater herbage accumulation rate on the W turves throughout most of the experiment, resulting in greater use of S (Table 4).

After *c.* 2 months of the stress treatments, there was a 0·47 decrease in herbage accumulation rate on the D treatment turves and a 1·21 increase in herbage accumulation rate on the wet (W) treatment turves in comparison with the control treatment. This indicated that the wetting treatment was highly beneficial to herbage accumulation under these environmental conditions. Norris (1982) also found increased herbage DM yields across a range of pasture species when swards were irrigated compared with control and droughted pastures. When combined with treading, however, which would occur in most grazing situations, the increase in herbage accumulation on the wet treatment turves was reduced to 0·29 greater than that of the control treatment. Approximately 2 months after the removal of the stress treatments, herbage accumulation on the D and W treatment turves was 0·22 and 0·16, respectively, greater than the control treatment. The WT turves, however, had a 0·32 smaller herbage accumulation rate than the control turves, indicating that the effects of treading, when combined with high soil moisture conditions, depressed herbage accumulation rate for at least 2 months after the cessation of treading. These results and the findings of others (Pande *et al.*, 2000) have important implications for the management of grazing livestock on wet soils. When soils are wet, careful consideration needs to be made of stock type, stocking rate and feed requirements to ensure minimal treading damage and an adequate supply of pasture throughout the period of grazing. Treading damage, if repetitive, may not only reduce pasture yields in the short-term but may also result in long-term effects on soil compaction and the ingress of low quality weed species.

If there is greater awareness of the direct impacts of stresses, such as drought and treading damage, on pasture production as well as the length of time it takes pastures to recover to pre-stress levels, it may assist with pasture management during and after stress events.

Conclusions

The leaf extension and tillering rates from this experiment suggest that moisture had a greater influence on leaf extension rate and treading on tillering rate. The results also indicated that moisture was the key factor limiting herbage accumulation on the C and D turves but, on the W and WT turves, nutrient availability was the limiting factor. That the drought treatment turves recovered quickly from the stress but the wet trodden turves took longer, indicate that, under the experimental conditions applied, the hill pasture turves are more resilient to the drying treatment than the wet and treading treatment. Two months after the cessation of the stress treatments, the wet and trodden turves had a 0·32 slower herbage accumulation rate than the control turves. The stocking density of hill pastures needs to be managed carefully, especially in wet conditions, to minimize any long-term decrease in herbage accumulation rate.

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